Food preference and effects of food type on the life history of some soil Collembola [1]

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Summary. Four species of onychiurid Collembola, six soil fungi and one actinomycete were isolated from soil, and were used in food preference tests in all possible combinations. *Protaphorura armatus* and *Tullbergia granulata* were selective feeders, showing very strong food preferences. *Tullbergia yosiii* and *Tullbergia iowensis* were general feeders, not discriminating between foods in most tests. One species in each of these groups was chosen for detailed life cycle studies in response to microbial foods. Diet (preferred vs. non-preferred foods) was found to affect *P. armatus* significantly. Preferred foods generally resulted in higher egg production and survival. However, shorter lifespans were compensated for by higher survival and egg production during early instars. In the general feeder, *T. yosiii*, few effects on life were observed. This study demonstrated that closely related collembolan species had totally different food preferences, and they responded differently to diet depending whether or not they showed preference to the food.

Key words: Soil Collembola, food preference, life cycle

Introduction

Soil Collembola are important in decomposition and nutrient cycling. Together with other microarthropods, they appear to influence decomposition primarily by grazing and dissemination of microflora (Seastedt 1984). Grazing activity can directly affect microbial metabolism and the relative importance of microflora in the soil community (Addison & Parkinson 1978; Hanlon & Anderson 1979; Parkinson et al. 1979; Visser et al. 1981; Newell 1984a, b).

Usually there are more than 30 collembolan species coexisting in temperate deciduous forest soils (Petersen 1982). These species must have some mechanism to partition their resources according to the competitive exclusion principle, although some studies indicated that this principle does not always apply to Collembola (Christiansen 1976). Niche partitioning cannot be explained by abiotic soil parameters (Moore et al. 1987), but several authors have suggested that food selectivity may be an important mechanism of niche separation (Schoener 1974; McMillan 1976; Matic & Koledin 1985).

Based on gut content analyses of field-collected individuals, Collembola have been regarded as general feeders, and foods of most species within a given habitat were found to be similar (Bödvarsson 1970; Gilmore & Raffensperger 1970; Anderson & Healey 1972; Takeda & Ichimura 1983). However, under laboratory conditions, Collembola showed clear food

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perferences when provided with a choice of foods (McMillan 1976; Visser & Whittaker 1977; Shaw 1988), and different collembolan species had different food preferences (Singh 1969; Walsh & Bolger 1990).

For each species, feeding on its preferred food should result in maximal fitness as suggested by optimal foraging theory (Pyke et al. 1977). In fact, the life history of Collembola is affected by the food type and its nutrient value (Snider 1971; Booth & Anderson 1979; Kurup & Prabhoo 1982; van Amelsvoort & Usher 1989).

The present experiments employed feeding preference tests and life history observations to assess the following biological traits among coexisting soil collembolan species: 1). Differences in food preferences; 2). Adaptive significance of preferences for microbial foods. 3). Differences between collembolan species in terms of life history in response to diets.

Materials and Methods

Species

All animals and microorganisms used in this study were extracted from soil in the Control site of the ELF ecological monitoring project (Snider & Snider 1987). The site was located in Dickinson County in Michigan's Upper Peninsula. It was a secondary growth deciduous forest dominated by maple and basswood (Snider & Snider 1987).

Soil was placed in Tullgren funnels for three days, and heat over the funnels was increased gradually by controlling voltage. Extracted Collembola were collected in culture jars containing a substrate of plaster of Paris and charcoal, and were periodically transferred to clean culture jars. Four coexisting species were selected: *Protaphorura armatus* (Tullberg), *Tullbergia granulata* Mills, *Tullbergia yosii* Rusek and *Tullbergia iowensis* Mills, because of their amenability to laboratory culture. All four are soil-dwelling Onychiuridae, and are parthenogenetic under laboratory conditions. Groups of ten adults were transferred to plastic culture jars provided with a 1:1 plaster of Paris:charcoal mixture (Snider et al. 1969). After eggs had been laid, the adults were killed and mounted on slides for species identification. Culture jars with eggs were kept for further use if all ten adults belonged to the same species, or were discarded if they contained two or more species. Animals were kept at room temperature (approximately 22 °C) and fed baker's yeast.

For isolation of soil fungi, potato dextrose agar (200 g potato, 20 g dextrose and 15 g agar per liter) was prepared. After autoclaving (120 °C, 15 minutes), 50 mg streptomycin sulfate was added to 250 ml PDA before pouring into Petri dishes. A drop of dilute soil suspension was spread over the surface of the hardened PDA. Cultures were kept at room temperature (approximately 22 °C) under an isolation hood, and were checked daily for microbial growth. Once growth of microorganisms had occurred, the single colony transference method was employed to purify the cultures. More than 50 isolates were obtained. Six fungi: *Mucor* sp., *Acremonium* sp., *Absidia* sp., *Humicola* sp., *Penicillium* sp. 1, *Penicillium* sp. 2 and an actinomycete, were identified and selected for food preference tests. These microorganisms were kept in agar slants and were periodically subcultured, so that all foods offered to the Collembola stemmed from the same colonies.

Food Preference Tests

All possible pairwise combinations of the six fungi and an actinomycete were tested against each other (21 total). The microorganisms were subcultured from slants to petri dishes with PDA and allowed to grow for one week. Autoclaved (120 °C, 30 minutes) plaster of Paris and charcoal were mixed with sterile distilled water and poured into 5-cm-diameter test jars, which were sterilized by immersion in 1% sodium hypochlorite (Clorox) solution and rinsed with sterile distilled water. Jars were allowed to set for three days before introducing microbial foods and animals.

Food offered to the Collembola consisted of agar discs (0.5 cm diameter) with microbial growth. Each test jar received two discs (two microbial species) placed on opposite sides of the jar perimeter. Sixteen adult animals which had been starved for 24 hours were introduced in the center of the jars, which were kept in the dark at room temperature. The number of individuals feeding on each food item was recorded five times at 12 hour intervals. Five or six replicates were used in each test.

Collembola had a tendency to aggregate around the food and stay there until it was exhausted. Possibly

the same animals remained near a food disc over two or more observation periods. Hence, the time variable was not independent over successive intervals, and was treated as repeated measurement.

The number of individuals feeding on each food item was converted to percent of total animals feeding and transformed to $\log_e$ (add) $[p/(1 - p)]$ for analysis. The homogeneity of the time variable (over time, no differences in the proportion of animals feeding on a given food item) was checked first. If not significant ($P > .05$), then multivariate analysis of variance was performed to test for food preference. If significant differences occurred over time, then data from each observation were tested separately. Generally there are three situations in which the time variable yielded significant differences: 1) One food item is preferred, but the degrees of preference are different over time. 2) A species shows preference at certain times but not at others. If three or four (out of five) times the species showed significant preferences, existence of a true perference was assumed. 3) A species prefers one food item at certain times but prefers another at other times.

Life History Studies

Based on results of food preference tests, two species, *P. armatus* and *T. yosiii*, were selected for life history studies. *Mucor* sp., *Acremonium* sp. and the actinomycete were offered as sole food sources to these animals. There was a total of six combinations (two collembolan and three microbial species). Each combination was replicated five times.

Age of experimental animals was standardized, by using individuals which had hatched within 24 hours. Twenty newly-hatched individuals were introduced to each replicate jar (5 cm diameter, 2.5 cm height), which contained a substrate of plaster of Paris and charcoal.

Microorganisms were kept in slants and were periodically subcultured in Petri dishes, where they were allowed to grow for one week. Agar discs (with mircobial growth) were then cut out (0.5 cm diameter) and placed in the center of the rearing jars. Food discs were changed every three or four weeks to reduce contamination and to prevent the possibility of starvation.

Rearing jars were incubated in the dark at a constant temperature of 20 °C. They were checked twice a week and moistened with sterile distilled water once a week. Individuals were transferred to new jars every six weeks to control contamination. An extra jar of every combination was kept in the same conditions as the test jars. When death of individauls in test jars caused unbalanced numbers of animals, replacements from the reserve cultures were used to keep numbers of animals approximately even. Growth, survival and egg production of the Collembola were monitored. The experiment lasted until average mortality reached 90%. During the experiment, five individuals were randomly selected from each jar, and their body length (including head) was measured every week for the first 25 weeks, once every two weeks thereafter. Exuviae produced by *T. yosiii* were counted and removed twice a week. Dead animals were recorded and removed. Eggs were counted and removed twice a week. Body length, survival and egg production were compared between three dietary treatments for *P. aramatus* and *T. yossiii*. In addition, production of exuviae by *T. yosiii* was analyzed. All statistical tests were performed using Tukey's test for each individual week. In the case of *P. armatus*, the group fed on *Acremonium* sp. had a shorter lifespan than the others, and *t*-tests were employed to compare the two remaining food treatments during the last few weeks.

Results

A. Food Preference

Each collembolan species showed different food preferences. *Protaphorura armatus* preferred both *Mucor* sp. and *Absidia* sp. over other food items in four out of six tests. It chose the actinomycete over both *Penicillium* sp. 1 and sp. 2, and *Humicola* sp. *Acremonium* sp. was preferred over both *Penicillium* sp. 2 and *Humicola* sp. *Penicillium* sp. 2 was consumed only when *Penicillium* sp. 1 was offered as an alternative. *Penicillium* sp. 1 and *Humicola* sp. were generally avoided (Table 1a).

Mucor sp., *Absidia* sp. and *Acremonium* sp. were preferred foods for *T. granulata*, over all other four food items. When the three readily consumed microbial foods were compared, no significant differences emerged (Table 1b). *Tullbergia granulata* did not select *Humicola*

Table 1. Results of feeding preference experiments. Symbolic abbreviations: >: Y axis food is significantly preferred over X axis food. <: X axis food is significantly preferred over Y axis food: =: no significant preference for either food

Y axis:	X axis: Absi.	Mucor	Acre.	Peni. 1	Peni. 2	Humi.	Acti.
a) Protaphorura armatus							
Absidia sp.	=	>	>	=	>	>	
Mucor sp.		>	>	=	>	>	
Acremonium sp.			=	>	>	=	
Penicillium 1				<	=	<	
Penicillium 2					=	<	
Humicola sp.						<	
actinomycete							
b) Tullbergia granulata							
Absidia sp.	=	=	>	>	>	>	
Mucor sp.		=	>	>	>	>	
Acremonium sp.			>	>.	>	>	
Penicillium 1				=	>	=	
Penicillium 2					=	=	
Humicola sp.						=	
actinomycete							
c) Tullbergia yostii							
Absidia sp.	=	=	=	>	=	=	
Mucor sp.		<	=	=	>	=	
Acremonium sp.			>	>	>	=	
Penicillium 1				=	=	=	
Penicillium 2					=	=	
Humicola sp.					.	=	
actinomycete							
d) Tullbergia iowensis							
Absidia sp.	=	=	>	=	=	>	
Mucor sp.		=	=	=	=	=	
Acremonium sp.			=	=	=	=	
Penicillium 1				<	=	=	
Penicillium 2					=	=	
Humicola sp.						=	
actinomycete							

sp., *Penicillium* sp. 2., or the actinomycete, and only fed on *Penicillium* sp. 1 more frequently than on *Humicola* sp.

Compared to *P. armatus* and *T. granulata*, both *T. yosiii* and *T. iowensis* were less discriminating in their choice of foods. *Tullbergia yosiii* and *T. iowensis* only showed six and three significant preferences out of 21 tests respectively. *Acremonium* sp. was the preferred food item for *T. yosiii*, over *Mucor* sp., *Humicola* sp., *Penicollium* sp. 1 and 2, but not over *Absidia* sp. and the actinomycete. *Tullbergia yosiii* also preferred *Mucor* sp. over *Humicola* sp., and *Absidia* sp. over *Penicillium* 2 (Table 1c). *Tullbergia iowensis* only showed preference for *Absidia* sp. over both *Penicillium* sp. 1 and the actinomycete, and for *Penicillium* sp. 2 over *Penicillium* sp. 1 (Table 1d). Results suggest that under controlled conditions, *T. yosiii* and *T. iowensis* are general feeders, and *T. granulata* and *P. armatus* are selective feeders.
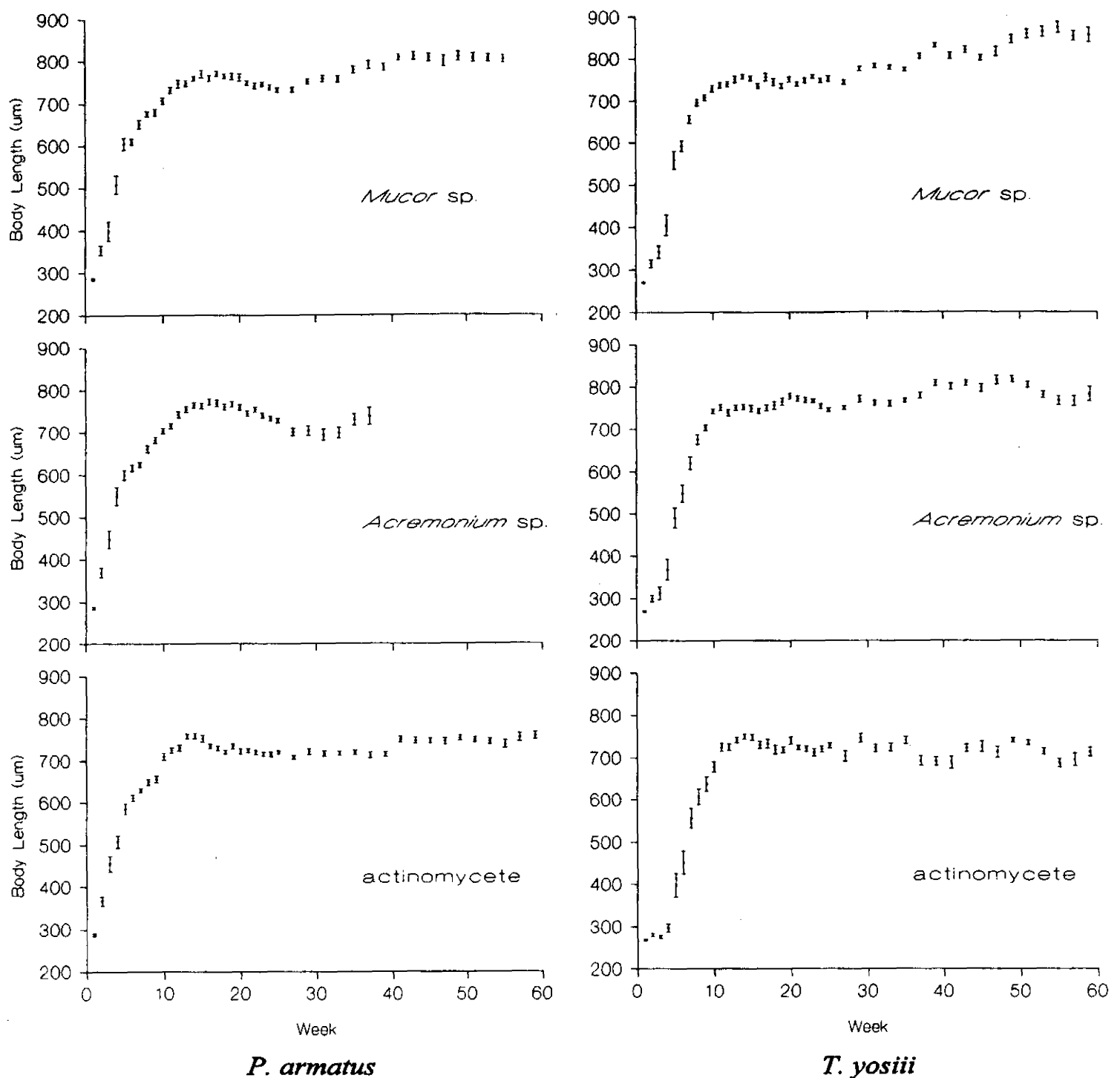
Fig. 1. Body length of *P. armatus* and *T. yosiii* fed on three different microbial foods. Vertical lines represent standard errors

B. Growth

Protaphorura armatus: Body length of *P. armatus* increased very rapidly at first, from newly hatched to fully developed in about 15 weeks (Fig. 1). After this period, average body length remained unchanged or even decreased slightly, depending on the food source they were offered. When fed *Mucor* sp., average body length fluctuated during this period. Fed *Acremonium* sp., it decreased gradually until week 30, then increased again. After reaching maximum size, individuals fed on the actinomycete decreased in size for a few weeks and then fluctuated until week 40. During the last few weeks of their life, body length usually increased again.

There were no significant size differences between animals feeding on three different food items during the first 15 weeks, with only minor, temporary exceptions. From week 16 until week 24, individuals feeding on the actinomycete were smaller than those feeding on either *Mucor* sp. or *Acremonium* sp. Late in their life (from week 27 to the end of the experiment), animals feeding on *Mucor* sp. had significantly larger bodies than those feeding on either *Acremonium* sp. or the actinomycete.

Tullbergia yosiii: After hatching, most individuals of *T. yosiii* increased in length very rapidly in the first ten weeks. Individuals fed *Mucor* sp. and *Acremonium* sp. kept increasing in size after the first ten weeks, although at a much slower pace. The size of individuals fed the actinomycete fluctuated during this period (Fig. 1).

Comparing animals feeding on the three different food items, those fed on the actinomycete usually had the shortest body length, although sometimes this was not statistically significant. Individuals fed on *Acremonium* sp. had larger bodies than those fed on *Mucor* sp. from week 18 to week 39, and in the last few weeks of the experiment, those fed on *Mucor* sp. showed significantly greater body length than individuals fed on *Acremonium* sp.

Tullbergia yosiii molted approximately 47 times during 63 weeks, at a relatively constant rate. There were no significant differences among the three treatments.

C. Survival

Protaphorura armatus: Survival rate of *P. armatus* was significantly influenced by food type (Fig. 2). Individuals fed on *Mucor* sp. had the highest survival rate. The survivorship curve of this group indicated a relatively constant rate of mortality independent of age. The average lifespan (based on 10% survival) was 55 weeks. The survival rate of individuals fed on *Acremonium* sp. was not significantly different from those offered *Mucor* sp. in the first 30 weeks. Mortality increased after week 25 and resulted in the shortest lifespan among the three treatments (average 37 weeks). Survival rate of juvenile animals fed on the actinomycete was relatively low, significantly so when compared to the group fed on *Mucor* sp. After the first five weeks, survival rate decreased very slowly and resulted in a longer lifespan (average 60 weeks).

Tullbergia yosiii: Differences in survival rates among the three groups were caused mainly by different juvenile mortalities (Fig. 3). The group fed on *Mucor* sp. had the lowest juvenile mortality and the group fed on the actinomycete experienced the highest. There was no statistical difference between the two groups fed on *Mucor* sp. and *Acremonium* sp. Their average lifespan were 63 and 61 weeks respectively. When the actinomycete was offered as food source the survival rate was significantly lower than when either *Mucor* sp. or *Acremonium* sp. were used. The average lifespan of individuals fed on the actinomycete was 56 weeks.
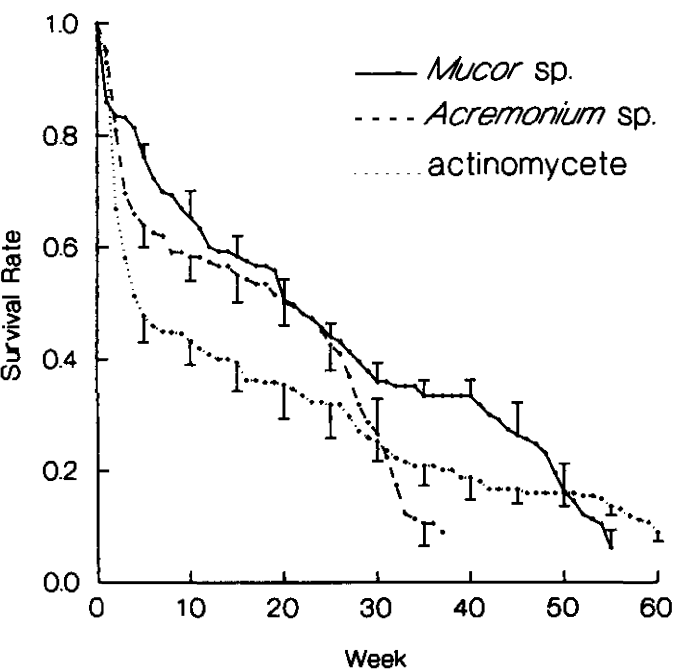

Fig. 2. Mean survival rates of *P. armatus* fed on three different microbial foods. Vertical lines represent standard errors
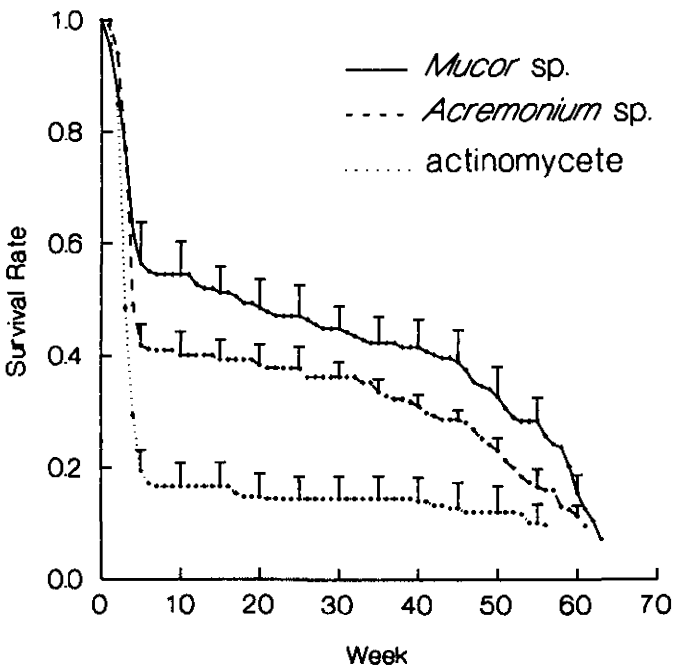
Fig. 3. Mean survival rates of *T. yosiii* fed on three different microbial foods. Vertical lines represent standard errors
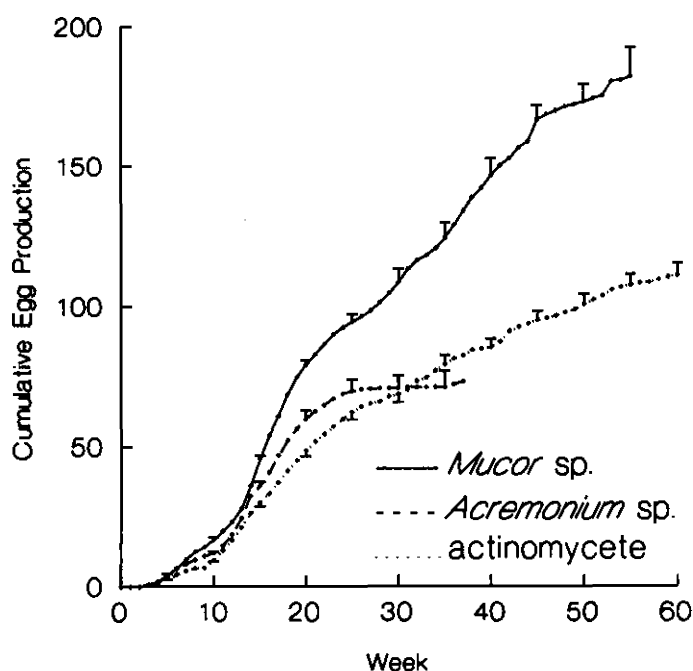
Fig. 4. Mean cumulative egg production per individual *P. armatus* fed on three different microbial foods. Vertical lines represent standard errors
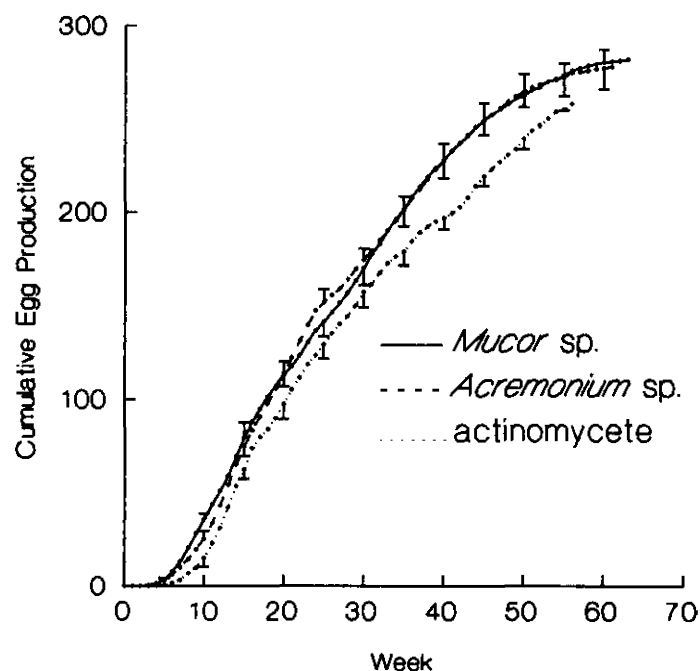

Fig. 5. Mean cumulative egg production per individual *T. yosiii* fed on three different microbial food. Vertical lines represent standard errors

D. Egg Production

Protaphorura armatus: *P. armatus* fed on all three microbial foods began producing eggs during the third week, numbers of eggs per individual increasing gradually toward a maximum during Week 14 or 15. Thereafter, mean weekly egg production decreased and became variable.

The group fed on *Mucor* sp. reached maximum egg production in week 15, with an average of 10 eggs per individual. From week 20 to 44, mean number of eggs fluctuated between 2 and 5, and after week 45 fewer than 2 eggs were produced per week. This group showed a higher cumulative egg production than the other two groups during their entire lifespan (Fig. 4), on average producing a total of more than 180 eggs per individual.

After reaching maximum egg production in week 14, individuals fed on *Acremonium* sp. gradually decreased their egg-laying activity. After week 27, this group usually did not produce any eggs at all. Cumulative egg production was generally higher than that of animals fed on the actinomycete, but only from week 8 to 22 (Fig. 4). Average total production per individual was 73 eggs in 37 weeks.

Individuals fed on the actinomycete showed a relatively constant weekly egg production from weeks 10 to 26. Egg production was highest in week 14 and was the lowest (about 5 per individual) among the three groups. Total egg prodcution, however, surpassed that of animals fed *Acremonium* sp. (Fig. 4). On average, 108 eggs were laid over an individual's lifespan.

Tullbergia yosiii: Individuals fed on *Mucor* sp. and *Acremonium* sp. began laying eggs in the third week, whereas those fed on the actinomycete began in the fourth week. All three groups reached maximum egg production in week 14. Overall, egg production among these three groups was very similar. Analysis of cumulative egg production (Fig. 5) yielded very few significant differences. In all three groups, an average of approximately 280 eggs per individual were laid over 63 weeks.

Discussion

Food preference tests showed that coexisting collembolan species have different food preferences. Results agreed with previous work dealing with two or more collembolan species (Singh 1969; Walsh & Bolger, 1990). The Collembola species used in their studies were from different families, some may live in totally different micro-habitats. Based on their food selectivity, the species in this study could be separated into two groups: selective

and general feeders. *Protaphorura armatus* and *T. granulata* were selective feeders, showing very strong food preferences when offered a choice. *Tullbergia yosiii* and *T. iowensis* were general feeders, not discriminating between foods in most of the tests. However, the two selective feeders showed differences in food selection. Both preferred *Mucor* sp. and *Absidia* sp., but *P. armatus* avoided *Acremonium* sp., while *T. granulata* accepted it to the same degree as the other two perferred microorganisms. *Protaphorura armatus* preferred the actinomycete over the other three food items, while *T. granulata* showed no preference for it. *Tullbergia granulata* exhibited a striking pattern in its selection of foods, grouping them into either preferred or not preferred foods. Given a choice between the two groups, it always clearly perferred one; given a choice within each group, it did not show any selectivity in most of the tests.

Although different microorganisms were used for food, results for *P. armatus* were comparable to those of Shaw (1988). In his study, *P. armatus* showed significant preferences in 43 tests out of 66 performed. In the present investigation, *P. armatus* showed 14 significant preferences in 21 tests. In both cases, approximately 2/3 of the tests yielded significant results.

When statistics are performed to test the significance of feeding preferences, one must be very careful in how to deal with the time variable. Because of the aggregative nature of these animals, the assumption of independence of successive observations is questionable. False assumptions of statistical independence lead to artificially high degrees of freedom, a condition termed "pseudoreplication" which permeates previous work on collembolan feeding preferences. Ideally each "observation" should be a separate experiment, but this would require an incredible amount of labor and resources (Shaw 1988). The method used here treated the time variable as a repeated measurement and reduced its degrees of freedom. Results are thus much more conservative as well as robust.

Snider (1971) stated that after a certain instar the size of *O. folsomi* fluctuated and bore no relation to the instar they were in. *Isotoma viridis* Bourlet lost weight, or live weight remained steady, during the period of senile molting (Zettel 1982). Variable body length was also observed in the present experiment. Previous studies have used body length or biomass to predict population growth. If age or instar of these animals were unknown, a serious problem could result. Considering *P. armatus* feeding on *Acremonium* sp., in week 31 its body length was almost the same as in week 10. In week 31 the animals were senile and had lost almost all of their fertility; in week 10, however, individuals were just beginning to reach maximum reproductive potential. The contribution of these two age groups to population growth would thus differ considerably, despite similar body size.

According to Snider (1974), *P. armatus* reached 10% survival rate between 200 and 420 days, and produced 98 to 124 eggs in its lifespan at temperatures ranging from 15 °C to 26 °C. Her results were very similar to those obtained here. The lifespan of individuals fed on three different foods ranged from 37 to 60 weeks, and cumulative egg production ranged from 73 to 182.

Food preference and life history data agreed perfectly in the case of *P. armatus*. The species favored *Mucor* sp. over the other two microbial foods. Fed on *Mucor* sp., it showed a much higher egg production than when reared on the other two foods. Its early survival rate was higher than when fed the actinomycete, and its lifespan was longer than when fed *Acremonium* sp. Results thus suggested that *P. armatus* preferred the food that was best for its life processes. Comparing *Acremonium* sp. to the actinomycete (both of which had equal preference ratings), *P. armatus* showed better early survival and higher egg production when fed on *Acremonium* sp., but a longer lifespan when fed the actinomycete. These data can be interpreted in terms of life history: higher survival and egg production early in life compensate for the shorter lifespan. A diet can be termed high quality when the cultured animals show the highest reproductive rate and the lowest mortality (Snider 1971). Therefore, *Mucor* sp. can be considered a high quality food for *P. armatus*.

Although *P. armatus* was identified as a selective feeder, in the broader sense the species can survive and reproduce well on a wide range of food items. Present data conflict, however, with results obtained by Walsh & Bolger (1990) in that *O. furcifer* achieved largest population size and fastest growth rates when fed on one of its least perferred foods.

It is not clearly understood why *T. yosiii* selected *Acremonium* sp. over *Mucor* sp. and other microbial foods in preference tests. There were no significant differences in survival, egg production and exuviae production when either *Acremonium* sp. or *Mucor* sp. were offered as food. Visser & Whittaker (1977), Addison & Parkinson (1978), Shaw (1988), Rusek (1989) and Schultz (1991) suggested that the existence of toxic materials resulted in avoidance behavior, which could explain avoidance of *Penicillium* sp. 1 and 2 by *T. yosiii*. Mills & Sinha (1971) found that *H. tullbergi* liked fungi with low mats but both *Acremonium* sp. and *Mucor* sp. used here had similar low mats. Bengtsson et al. (1988) observed that odors of fungi played an important role in attracting Collembola. Schultz (1991) found that hyphal diameter and cell wall thickness bore no relationship to food selection by Collembola. It can only be speculated that some other physical or chemical characteristics of the two food items may have induced the species to favor *Acremonium* sp. over *Mucor* sp. From a nutritional point of view, these two food items did not cause any differences in growth, survival, egg and exuviae production.

The only disadvantage when *T. yosiii* fed on the actinomycete was the higher juvenile mortality. Once individuals survived to the adult stage, the actinomycete provided almost the same nutritional value as the other two foods in terms of survival rate, egg production and molting frequency. It is concluded that, as a general feeder, *T. yosiii* can grow equally well on different foods.

Van Amelsvoort & Usher (1989) found that *Folsomia candida* adopted a "fuzzy" life history strategy along the r-K spectrum. It appeared to be able to alter its position in response to feeding conditions: r-selected when conditions were good, but apparently K-selected when conditions were poor. The theory is only relevant to *P. armatus* feeding on *Acremonium* sp. and the actinomycete in this study. According to their theory, *Acremonium* sp. should be considered a higher quality food for *P. armatus* than the actinomycete, because feeding on *Acremonium* sp. speeded up life processes by means of higher early egg production and a short lifespan.

Potato dextrose agar, a nutrient rich medium, was used for isolating and culturing fungi for both feeding preference and life history studies. Fresh cultured fungi were used throughout the experiments to standardize conditions. Fungal grazing by Collembola in natural habitats occurs at a much more complex level. The availability and accessibility of fungal species may differ along temporal and spatial lines. Fungi grown from different substrates may also affect their palatability to Collembola. The preference of Collembola may be adjusted depending upon fungal community species composition, abundance and palatability of preferred fungal species (Visser & Whittaker 1977; Bengtsson et al. 1985).

The collembolan species used in this experiment are closely related and live in a similar habitat. They all belong to family Onychiuridae, with three species in *Tullbergia*, subfamily Tullberginae; and the other in *Protaphorura*, subfamily Onychiurinae. They were usually found together in single 5-cm diameter soil core samples taken from our study site. This study demonstrated that closely related collembolan species had totally different food preferences. They responded differently to their diet depending on food preference. It may be of ecological importance for coexisting species to separate their resources, and adopt different feeding behaviors which are reflected in their life-history processes.

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